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Studien ueber die Myxosporidien der norwegischen Seefische und ihre Verbreitung

Zool. Jahrb. 34 Abt. f. Syst., 1-50 (1912)

Studies concerning the Myxosporidia of Norwegian marine Fishes, and their distribution

by Prof. M. AUERBACH of Karlsruhe in Baden

(from the Biological Station at Bergen, Norway)

with Plates 1-5 and 5 illustrations in the text

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In my work entitled "Unsere heutigen Kenntnisse ueber die geographische Verbreitung der Myxosporidien" ("Our current knowledge of the geographic distribution of the Myxosporidia", Zool. Jahrb. vol. 30, Syst., 1911) I compiled all of the data known to me at that time concerning the geographic distribution of these parasites. I was obliged to conclude that they were fairly evenly distributed along the European coasts as far as they had been investigated, that the parasitic species probably occured wherever their hosts were found, and that they perhaps even could attack other fishes in regions where these hosts were absent. At that time, my evidence for such extensive distribution came chiefly from

the Mediterranean and Atlantic coasts, which had been best studied in this respect and had very similar faunas of Myxosporidia.

Hitherto the North has been only very poorly studied for parasites belonging to the Myxosporidia; yet even in my work cited above, I was able to refer to certain cases indicating that the range of the fauna in question could be traced at least into that region also, if only the appropriate investigations would be undertaken. The examples given then related to the occurence of Leptotheca parva THÉL. at Marseilles, Le Croisic and Bergen, and of Ceratomyxa sphaerulosa THÉL. at Roscoff, Wimereux and Bergen.

I was therefore much delighted when I obtained another opportunity to study the Norwegian fish in 1911. It is a pleasant duty for me to express again on this occasion my sincerest gratitude to our Karlsruhe Natural Sciences Association and our generous Ministry of Culture and Education for granting the necessary funds for my expedition.

My expedition was concerned quite specifically with the study of the geographic distribution of the Myxosporidia in marine fishes along the entire Norwegian coast from Kristiania to Vadsö; and since I had only one month for this study, I had to arrange my travel plans in order to cover the entire coast within this period and collect fish at the suitable stations. I therefore traveled on the mail boat "Mercur" of the "Bergenske Dampskibselskab" in Bergen from

Hamburg to Vadsö (Kirkenes) and back as far as Trondheim, and then returned by rail to Kristiania. My friend, doctoral candidate K. HUMMEL accompanied me as my assistant. He was tirelessly helpful to me in collecting and processing the material, and also collected additional fish afterwards at Kristiania and in the Kristiania Fjord; I should like again on this occasion to thank him heartily for his collaboration.

I had thought it impossible from the start that I should be able to collect even a nearly complete assortment of fish material within the short time available, and so I had intended to study in large numbers only the most common and most frequently fished species; of course, all other attainable species were to be included as well in the study. Initially, I expected to procure my fish only at the quays of the various Norwegian fish markets, and a very good 3
number of fish were in fact obtained from this source. However, it was very troublesome that fish could be bought everywhere only in the morning, and even at important locations such as Hammerfest, I could not find a single fish in the afternoon. Consequently, if I had remained dependent only on this source, I should not have been able to bring home a large number of fish. Fortunately, the gap was filled excellently when the passengers and crew of the "Mercur" supplied me with oustanding material for study by fishing avidly at every station, so that often much toil was required quickly to process the fish. Indeed, I am greatly indebted

to the captain, officers, and crew, and also my Norwegian fellow-travelers for constantly striving in every conceivable way to advance my investigations as much as possible; without their support, I could not have accomplished half as much.

The freshly caught fish were subjected immediately to close inspection inside and out; skull bones and cartilage, eyes, and gills were examined and, if suspect, preserved immediately in 5% formalin; the gall bladders of all fish, and the urinary bladders of most were fixed in 5% formalin or sublimate-alcohol-glacial acetic acid and prepared for laboratory study.

I. Geographic section

As I have already mentioned above, I had to concentrate upon the most common and frequently fished species, and attempt to obtain as many fish of these species as possible from as many different locations as possible. Accordingly, the bulk of my material comprised Gadidae, including Gadus callarias, G. virens and G. aeglefinus; also a good number of flatfish (Pleuronectes platessa) and Salmonidae (Trutta salar) were examined. If we add to these the fish which I studied during my previous investigations in Bergen, the complete list of the material which I employed will appear as shown in Table I. (This table lists the number of individuals of each species examined; those infected with Myxosporidia, and the provenance of the fish are shown separately.)

Thus, the total number of fish investigated hitherto 4
is 679. The Myxosporidia found in these fish are listed in Table II, and the coastal stations where the fish were taken are shown in Table III.

A comparison of the location of these stations on the 5
accompanying map (Plate 1) will quickly show that the fishing sites are distributed fairly reguarly along the entire coast. In the North, the stations are closer together, because here the steamers stop more often, and at the same time fishing is much better than farther south.

For general orientation, I have provided one more, final list, showing the fishes studied, the places where they were caught, the Myxosporidia found in them, and the body organs in which the parasites were found. This list (Table IV) will help greatly to summarize and simplify my exposition.

Now before I turn to a somewhat more detailed discussion of the results shown in this table, I should like to emphasize that I am far from considering my findings in this study to be complete and definitive. I myself am most aware of the defects and omissions, and I know well that my work can only be considered as a minor attempt to clarify the distribution of the northern Myxosporidia. Longer and more strenuous study will be needed before we can assert that all of the major questions which interest us are resolved, and certainly also many of my data will have to be supplemented and revised. However, since at present we have a total lack of knowledge

Table I.

Lfd. No.[1]		Exemplar[2]	Lfd. No.[1]		Exemplar[2]
1.	*Luciopercа sandra* L.	1	19.	*Gadus pollachius* L.	2
2.	*Sebastes viviparus* KRÖYER	16	20.	— *poutassou* RISSO	2
3.	— *marinus* L.	2	21.	— *minutus*	1
4.	— *dactylopterus* DE LA ROCHE	2	22.	*Molva vulgaris* FLEM.	16
5.	*Trigla gurnardus* L.	5	23.	— *byrkelange* WALB.	1
6.	*Scomber scombrus* L.	20	24.	*Brosmius brosme* ASCAN.	11
7.	*Labrus mixtus* L.	4	25.	*Phycis blennioides*	1
8.	— *rupestris* L.	2	26.	*Onos tricirrhatus*	1
9.	— *bergylta* L.	3	27.	*Trutta trutta* L.	1
10.	*Anarrhichas lupus* L.	8	28.	— *salar* L.	13
11.	*Centronotus gunellus*	1	29.	*Argentinus silus* ASCAN.	6
12.	*Gobius niger* L.	2	30.	*Clupea harengus* L.	15
13.	*Callionymus lyra*	2	31.	— *sprattus* L.	56
14.	*Cyclopterus lumpus* L.	2	32.	*Pleuronectes platessa* L.	28
15.	*Gadus callarias* L.	144	33.	— *flesus* L.	5
16.	— *aeglefinus* L.	70	34.	— *limanda*	1
17.	— *virens* L.	215	35.	*Hippoglossus vulgaris* FLEM.	3
18.	— *merlangus* L.	14	36.	*Hippoglossoides limandoides*	3

1-serial number 2-specimens

Table II.

I. Monosporea: 0.	**III. Disporea: 6.**
II. Miktosporea: 8.	1. *Leptotheca macrospora* AUERB.
1. *Myxidium bergense* AUERB.	2. — *parva* THÉL.
2. — *incurvatum* THÉL.	3. — *informis* AUERB.
3. — *inflatum* AUERB.	4. — *longipes* AUERB.
4. — *procerum* AUERB.	5. *Ceratomyxa drepanopsettae* AWER.
5. — *oviforme* PARISI	6. — *sphaerulosa* THÉL.
6. *Sphaeromyxa hellandi* AUERB.	**IV. Polysporea: 1.**
7. *Zschokkella hildae* AUERB.	1. *Myxobolus aeglefini* AUERB.
8. *Sphaerospora divergens* THÉL.	

Table III.

1.	Kristiania	10.	Rörvik	19.	Harstad	28	Mehavn
2.	Tjömö	11.	Mosjöen	20.	Rossfjord	29.	Finkongkjeilen
3.	Kristiansand	12.	Torghatten	21.	Skjervö	30.	Smalfjorden
4.	Stavanger	13.	Vikholmen	22.	Bergsfjord	31.	Baadsfjord
5.	Bergen	14.	Grönöy	23.	Nusfjord	32.	Makur
6.	Aalesund	15.	Bodö	24.	Hasvik	33.	Vardö
7.	Kristiansund	16.	Kabelvaag	25.	Hammerfest	34.	Kiberg
8.	Trondhjem	17.	Svolvaer	26.	Honningsvaag	35.	Kirkenes
9.	Abelvaer	18.	Lödingen	27.	Skjötningsberg		

Table IV.

Lfd. No.	Fisch	Herkunft	Parasit	Infizierte Organe	Anzahl der infiz. Expl.	Anzahl der unters. Expl.
1.	*Lucioperca sandra*	Kristiania, 12./8. 1911	—	—	—	1
2.	*Sebastes viviparus*	Bergen, 2./9. 1908	*Leptotheca macrospora* Auerb.	Gallenblase	1	5
			Myxidium bergense? Auerb.	"	1	
		„ 15./5. 1909—3./6. 1909	Unbestimmbare Myxosporidie ♀	"	6	7
		Kristiansund, 8./7. 1911	*Leptotheca macrospora* Auerb.	"	2	3
			Myxidium bergense Auerb.	"	1	
		Trondhjem, 10./7. 1911	Unbestimmbare Myxosporidie ♀	"	1	1
3.	*Sebastes marinus*	Bergen, 11./9. 1908	—	—	—	1
		„ 11./5. 1909	—	—	—	1
4.	*Sebastes dactylopterus*	„ 26./5. 1909	*Leptotheca macrospora* Auerb.	Gallenblase	1	2
5.	*Trigla gurnardus*	„ 16./9. 1908	—	—	—	1
		„ 11./6. 1909	—	—	—	1
		Tjömö, 2./8. 1911	—	—	—	3
6.	*Scomber scombrus*	Bergen, 7./9. 1908	*Leptotheca parva* Thél.	Gallenblase	4	4
		„ 25./5. 1909	"	"	1	2
		Kristiansand, 3./7. 1911	"	"	1	9
		Stavanger, 4./7. 1911	"	"	2	3
		Tjömö, 2./8. 1911	—	—	—	2
7.	*Labrus mixtus*	Bergen, 5./9. 1908	—	—	—	1
		„ 2./6. 1909	—	—	—	2
		Kristiansand, 3./7. 1911	—	—	—	1
8.	*Labrus rupestris*	Bergen, 5./9. 1908	—	—	—	2
9.	*Labrus bergylta*	„ 22./5. 1909	—	—	—	1
		„ 2./6. 1909	—	—	—	2
10.	*Anarrhichas lupus*	„ 3./9. 1908	*Myxidium bergense?* Auerb.	Gallenblase	1	1
		„ 13./5. 1909	—	—	—	1
		Trondhjem, 10./7. 1911	—	—	—	3
		„ 11./7. 1911	—	—	—	3
11.	*Centronotus gunellus*	Torghatten, 12./7. 1911	*Sphaeromyxa hellandi* Auerb.	Gallenblase	1	1
12.	*Gobius niger*	Bergen, 15./9. 1908	—	—	—	2
13.	*Callionymus lyra*	Bergen, 19./6. 1909	*Myxidium incurvatum* Thél.	Gallenblase	2	2
			Myxidium	Harnblase	—	
14.	*Cyclopterus lumpus*	„ 12./9. 1908	*Myxidium inflatum* Auerb.	Gallenblase ♀	1	1
		„ 29./5. 1909	—	—	—	1
		„ 31./8. 1908	—	—	—	1
15.	*Gadus callarias*	„ 12./5.—12./6. 1909	*Myxidium oviforme* Parisi	Gallenblase ♀	1	6
			Zschokkella hildae Auerb.	Harnblase	2	
		Kristiania, 12./8. 1911	—	—	—	1
		Tjömö, 4. u. 7./8. 1911	—	—	—	2
		Kristiansund, 8./7. 1911	*Myxidium oviforme* Parisi	Gallenblase ♂	1	2
			" " jung?	"	1	
		Trondhjem. 10./7. 1911	" " jung?	"	2	2
			Zschokkella hildae Auerb., jung	Harnblase	1	
		Abelvaer, 12./7. 1911 und 27./7. 1911	*Myxidium oviforme* Parisi ad. u. jung?	Gallenblase ♀	3	3
			Zschokkella hildae Auerb.	Harnblase	1	
			Myxobolus aeglefini Auerb.	Auge	1	
		Rörvik, 12./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	2	9
			" *oviforme* Parisi, jung?	"	4	
		Kabelvaag, 25./7. 1911	" Parisi, jung?	"	2	2
			Zschokkella hildae Auerb.	Harnblase	1	
		Lödingen, 14./7. 1911	*Myxobolus aeglefini* Auerb.	Auge und Schädel	1	1
		Skjervö, 16./7. 1911	*Myxidium oviforme* Parisi, jung?	Gallenblase ♀	1	9
			Zschokkella hildae Auerb.	Harnblase	9	
		Bergsfjord, 16./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	2	4
			" *oviforme* Parisi, jung?	"	2	
			Zschokkella hildae Auerb.	Harnblase	4	
		Nusfjord, 16./7. 1911	*Myxidium oviforme* Parisi, jung?	Gallenblase ♀	1	1
			Zschokkella hildae Auerb.	Harnblase	1	
		Hasvik, 16./7. 1911 u. 22./7. 1911	*Myxidium oviforme* Parisi, jung?	Gallenblase ♀	2	5
			" " ad. und jung	"	3	4
		Hammerfest, 17./7. 1911	*Zschokkella hildae* Auerb.	Harnblase	4	
		Honningsvaag, 17./7. 1911	*Myxidium oviforme* Parisi, jung?	Gallenblase ♀	26	30
			Zschokkella hildae Auerb.	Harnblase	16	
		Finkongkjeilen, 18./7. und 21./7. 1911	*Myxidium oviforme* Parisi, jung?	Gallenblase ♀	8	10
			Zschokkella hildae Auerb.	Harnblase	5	

Lfd. No.	Fisch	Herkunft	Parasit	Infizierte Organe	Anzahl der infiz. Expl.	Anzahl der unters. Expl.	
		Smalfjorden, 18./7. 1911	*Myxidium oriforme* Parisi, jung?	Gallenblase ♂	8	9	
			Zschokkella hildae Auerb.	Harnblase ♂	8		
		Baadsfjord, 18./7. 1911	*Myxidium oriforme* Parisi, jung?	Gallenblase ♀	8	11	
			Zschokkella hildae Auerb.	Harnblase ♂	9		
		Makur, 18./7. 1911			2	3	
		Vardö, 19./7. 1911	*Myxidium oviforme* Parisi ad. u. jung	Gallenblase ♀	13		
			Myxobolus aeglefini Auerb.	Auge und Schädel	1	25	
			Zschokkella hildae Auerb.	Harnblase ♂	23		
		Kiberg, 20./7. 1911	*Myxidium oviforme* Parisi, jung?	Gallenblase ♂	3	4	
			Zschokkella hildae Auerb.	Harnblase ♂	3		
16.	*Gadus aeglefinus*	Bergen, 28./8.—20./9. 1908	—	—	—	13	
		„ 25./5. 1909	—	—	—	1	
		Kristiania, 12./8. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	1	2	
		Kristiansund, 8./7. 1911	*Zschokkella hildae* Auerb.	Harnblase ♂	1	1	
		Trondhjem, 10. u. 11./7. 1911	*Myxidium bergense* Auerb.? jung	Gallenblase ♂	2	2	
			Zschokkella hildae Auerb.	Harnblase ♂	2		
		Abelvaer, 27./7. 1911	*Myxidium bergense* Auerb.? jung	Gallenblase ♀	2	2	
			Myxobolus aeglefini Auerb.	Auge	1		
		Rörvik, 12./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	1	1	
		Mosjöen, 26./7. 1911	„ „ Auerb. ad. u. juv.		4	4	
			Zschokkella hildae Auerb.	Harnblase ♂	4		
		Vikholmen, 13./7. 1911			2	4	
		Grönöy, 25./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	5	5	
			Zschokkella hildae Auerb.	Harnblase ♂	4		
		Bodö, 25./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	2	2	
			Zschokkella hildae Auerb.	Harnblase ♂	1		
		Nusfjord, 16./7. 1911	*Myxidium bergense* Auerb., jung	Gallenblase ♀	13	13	
			Zschokkella hildae Auerb.	Harnblase ♂	8		
		Finkongkjeilen, 18./7. 1911	*Myxidium bergense* Auerb., jung	Gallenblase ♀	1	1	
			Zschokkella hildae Auerb.	Harnblase ♂	1		
		Makur, 18. u. 20./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♂	11	11	
			Zschokkella hildae Auerb.	Harnblase ♂	6		
		Vardö, 19./7. 1911	*Myxidium bergense* Auerb., jung	Gallenblase ♀	8	8	
			Zschokkella hildae Auerb.	Harnblase ♂	7		
17.	*Gadus virens*	Bergen, 29./8.—25./9. 1908	*Myxidium bergense* Auerb.	Gallenblase ♀	14	25	mittelgroße Expl.
		„	—	—	—	1	junges Expl.
		„ 10./5.—23./6. 1909	*Myxidium bergense* Auerb.	Gallenblase ♂	31	57	mittelgroße Expl.
			Zschokkella hildae Auerb.	Harnblase ♂	3		
			Myxidium bergense Auerb.	Gallenblase ♀	4	44	junge Expl.
			Zschokkella hildae Auerb.	Harnblase ♂	8		
			„		1	3	90 cm lange Expl.
			Myxidium bergense Auerb.?	Gallenblase ♀	12	14	künstlich infizierte junge Versuchsfische
		Kristiansand, 3./7. 1911	„	„	2	5	ganz junge Infektion? Nicht sicher zu sagen
		Stavanger, 4./7. 1911	„	„	3	3	
		Kristiansund, 8./7. 1911			2	3	
			Zschokkella hildae Auerb.	Harnblase ♂	3		
		Trondhjem, 10./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♂	3	3	
		Abelvaer, 27./7. 1911			3	3	
			Zschokkella hildae Auerb.	Harnblase ♂	1		
		Bodö, 25./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	6	6	
			Zschokkella hildae Auerb.	Harnblase ♂	3		
		Kabelvaag, 25./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	5	5	1 unsicher, ganz jung
			Zschokkella hildae Auerb.	Harnblase ♂	2		
		Svolvaer, 14./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	6	6	
			Zschokkella hildae Auerb.	Harnblase ♂	1		
		Harstad, 21./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	3	3	
			Zschokkella hildae Auerb.	Harnblase ♂	3		
		Skjötningsberg, 21./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	5	5	
			Zschokkella hildae Auerb.	Harnblase ♂	3		
		Vardö, 20./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	7	8	
			Zschokkella hildae Auerb.	Harnblase ♂	5		
		Kirkenes, 19./7. 1911	*Myxidium bergense* Auerb.	Gallenblase ♀	1	1	
		Bodö, 25./7. 1911			1	1	großes Expl.
			Zschokkella hildae Auerb.	Harnblase ♂	1		

Lfd. No.	Fisch[2]	Herkunft[3]	Parasit[4]	Infizierte Organe[5]	Anzahl der infiz. Expl.[6]	Anzahl der unters. Expl.[7]	
		Hammerfest, 17./7. 1911	*Myxidium bergense* Auerb.	Gallenblase[8]	2	3	große Expl.[21]
			Zschokkella hildae Auerb.	Harnblase[10]	3		
		Vardö, 20./7. 1911	*Myxidium bergense* Auerb.	Gallenblase[8]	3	3	große Expl.[21]
		Harstad, 24./7. 1911		„	12	12	kleine, junge Expl.[22]
			Zschokkella hildae Auerb.	Harnblase[10]	6		
		Honningsvaag, 17./7. 1911	*Myxidium bergense* Auerb.	Gallenblase[8]	1	1	
			Zschokkella hildae Auerb.	Harnblase[10]	1		
18	*Gadus merlangus*	Bergen, 28./8. 1908	Unbestimmbare Myxosporidie[9]	Gallenblase[8]	1	3	
		„ 15./5.—12./6. 1909	*Lepthotheca sp.* od. *Ceratomyxa sp.*	„	4	6	
		Tjömö, 2.—7./8. 1911		„	1		
			Leptotheca informis Auerb.	„	1	5	
			Myxidium bergense Auerb.	„	2		
19.	*Gadus pollachius*	Bergen, 16./9. 1908	—	—	—	2	
		„ 11./6. 1909	—	—	—		
20.	— *pontassou*	„ 14./9. 1908	—	—	—	2	
21.	— *minutus*	„ 15./5. 1909	—	— [14]	—	1	
22.	*Molca vulgaris*	„ 28./8. 1908	*Myxobolus aeglefini* Auerb.	Schädelknorpel	1	1	
		„ 3./9. 1908	*Leptotheca sp.*	Gallenblase[8]	2	3	
			Myxobolus aeglefini Auerb.	Schädelknorpel[14]	1		
			Sphaeromyxa hellandi Auerb.	Gallenblase[8]	2	2	
		„ 15./5. 1909	*Lepthotheca sp.*	„	1	1	
		„ 19./5. 1909	*Leptotheca informis* Auerb.	„	1	1	
		Tjömö, 4./8. 1911	„	„	1	1	[23]
		Aalesund, 7./7. 1911	—	—	—	6	nur Köpfe unters.
		Trondhjem, 10./7. 1911	—	—	—	1	
23	*Molca byrkelange*	Bergen, 16./9. 1908	—	—	—	1	
24	*Brosmius brosme*	„ 28./7. 1908	—	—	—	9	
		„ 3./9. 1908	*Leptotheca sp.*	Gallenblase[8]	1	1	
		„ 15./5. 1909	*Sphaeromyxa hellandi* Auerb.	„	1	1	
25	*Phycis blennioides*	„ 26./5. 1909	*Zschokkella hildae* Auerb.	Harnblase[10]	1	1	
26.	*Onos tricirrhatus*	„ 11./6. 1909	—	—	—	1	
27.	*Trutta trutta*	„ 6./7. 1911	—	—	—	1	
28.	*Trutta salar*	Mosjöen, 26./7. 1911	—	—	—	1	
		Bodö, 13./7. 1911	—	—	—	5	
		Rossfjord, 14./7. 1911	*Myxidium oriforme* Parisi	Gallenblase[8]	1	3	
		Sjötningsberg, 21./7. 1911	—	—	—	4	
29.	*Argentinus silus*	Bergen, 3./9. 1908	—	—	—	2	
		„ 26./5. 1909	*Myxidium procerum* Auerb.	Gallenblase[8]	2	4	
30.	*Clupea harengus*	„ 31./8.—4./9. 1908	*Ceratomyxa sphaerulosa* Thél.	„	1	15	
31	— *sprattus*	„ 17./9. 1908	—	—	—	56	
32.	*Pleuronectes platessa*	Kristiania, 12./8. 1911	Unbestimmbare Myxosporidie[9]	Gallenblase[8]	1	6	
		Rörvik, 12./7. 1911	*Ceratomyxa drepanopsettae* Awer.	„	3	4	
			Myxidium bergense Auerb.	„	1		
		Kabelvaag, 25./7. 1911	—	—	—	4	
		Svolvaer, 14./7. 1911	Unbestimmbare Myxosporidie[9]	Gallenblase[8]	1	10	
			Myxidium sp.?	„	2		
		Mehavn, 21./7. 1911	—	—	—	3	
		Baadsfjord, 20./7. 1911	Unbestimmte Myxosporidie[9]	Gallenblase[8]	1	1	
33.	*Pleuronectes flesus*	Tjömö, 2./8. 1911	? *Ceratomyxa drepanopsettae* Awer.	„	4	5	
34.	— *limanda*	Bergen, 14./5. 1909	—	—	—	1	
25.	*Hippoglossus vulgaris*	„ 26./5. 1909	—	—	—	1	
		Kabelvaag, 25./7. 1911	*Ceratomyxa drepanopsettae* Awer.	Gallenblase[8]	2	2	
36.	*Hippoglossoides limandoides*	Smalfjorden, 18./7. 1911	„	„	3	3	
			Sphaerospora divergens Thél.	Harnblase[10]	1		

1-serial number 2-fish 3-provenance 4-parasite 5-infected organs 6-number of specimens infected 7-number of specimens examined 8-gall bladder 9-undetermined Myxosporidium 10-urinary bladder 11-and 12-juvenile 13-eye and skull 14-skull cartilage 15-medium-sized spec. 16-juvenile spec. 17-90 cm long 18-experimentally infected juveniles 19-very young; infection? uncertain 20-uncertain, very young 21-large spec. 22-small, juvenile spec. 23-only heads examined 24-eye

on this subject, my few findings and hypotheses will make a beginning which, hopefully, can be continued as soon as possible by myself or by others.

If the Myxosporidia of Norwegian fishes listed in Table II are compared with my previous data (1-7), the most striking feature is that the number of new species for Norway has risen only by very few, viz., 3-5. (I have listed only the securely identified forms, to which may perhaps be added also a new Ceratomyxa from Pleuronectes flesus, possibly not identical with C. drepanopsettae AW., and a member of the same genus from Gadus merlangus, which could correspond with a parasite of the same fish in the Mediterranean. I shall attempt to resolve this question in Part II of the present study.)

Among these new forms, the occurence of Ceratomyxa drepanopsettae AW. in the fishes of the Norwegian coast was predictable; indeed, it was described by AWERINZEW (8) in directly neighboring areas (Murman Coast). The latter author found this form in Pleuronectes platessa L. and Drepanopsetta platessoides FABR.; I can add as new hosts Hippoglossus vulgaris, Hippoglossoides limandoides, and perhaps also Pleuronectes flesus; however, I am not altogether certain with repect to Pleuronectes flesus. If we assume that the parasite of this fish also belongs to our species, then its range would fairly probably extend along the entire coast of Norway from Tjömö to the Murman Coast. The sites where it has been found would

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then be Tjömo, Rörvik, Kabelvaag and the Murman Coast. On the other hand, if we are more conservative and do not accept Pl. flesus as a host, then according to our present knowledge, the range extends only to Rörvik; however, I have no doubt that further research will reveal this species also farther south.

A matter of far greater interest is the occurrence of two other species, viz., Myxidium oviforme PARISI and Sphaerospora divergens THÉL.

Myxidium oviforme was described only very recently, by PARISI (19). This author found the parasite in the gall bladder of Coris julis GTHR. and Apogon rex-mullorum CUV. from the vicinity of Naples. I found the parasite and free spores in Gadus callarias from Bergen, Kristiansund, Abelvaer, Hammerfest and Vardö, i.e., along all of the Norwegian coast. However, in many fish from other stations, also young vegetative forms without spores were found which I view as belonging to our parasite, so that the species is quite common in G. callarias, with approximately 61.8% of all fish infected; finally, also its occurence in a salmon from Rossfjord should be mentioned. Thus, the range of M. oviforme is very extensive, from Naples to Vardö. There is still a gap within this range along the entire Atlantic coast of France, in the southern part of the North Sea, and off England; but in any case, sites will be discovered also here in time. As far as I know, Apogon rex-mullorum CUV. occurs chiefly in the

Mediterranean, whereas Coris julis GTHR. extends into the North Sea, so that there are extensive points of contact between it and Gadus callarias. Today, of course, we can 13
not yet determine how the parasite spread, whether primary and secondary hosts should be assumed, and if so, which host is primary, etc.

My finding of Sphaerospora divergens THÉL. is even more remarkable. I found this parasite in the urinary bladder of a specimen of Hippoglossoides limandoides far to the North, in Tanafjord (Smalfjorden); thus, a new host has been found for this species as well as a new site, since previously only Blennius pholis L., Crenilabrus melops L. (THÉLOHAN 23) and Cr. pavo C.V. (PARISI 19) were known as hosts. The parasite has been found near Naples (PARISI 19), Concarneau and Roscoff (THÉLOHAN 23), and Smalfjorden (AUERBACH). Although these sites are very far apart, they are in three distinct, but related sea basins--the Mediterranean, the Atlantic Ocean, and the Arctic Ocean; and I believe that it would not be premature to conjecture that eventually, the species will be found also at intervening sites, so that its range would then be continuous along the entire European coast.

A very fine example of unbroken distribution along the entire coast is provided by Myxidium bergense AUERB., which I was able to study in such large quantities that it can be discussed at greater length. This parasite was

previously known only from the gall bladder of Gadus virens. To this host, I can now add with a fair degree of certainty (1) Sebastes viviparus, (2) Anarrhichas lupus, (3) Gadus aeglefinus, (5) Gadus merlangus and (6) Pleuronectes platessa. The places near which the parasite has been found are as follows:

> Kristiania, Tjömö, Kristiansand, Stavanger, Bergen, Kristiansund, Trondhjem, Abelvaer, Rörvik, Mosjöen, Grönöy, Bodö, Kabelvaag, Svolvaer, Harstad, Bergsfjord, Nusfjord, Hammerfest, Honningsvaag, Skjötningsberg, Finkongkjeilen, Makur, Vardö, Kirkenes.

Comparing these locations with the map (Plate 1) leaves no doubt of the continuous distribution of the species.

For some hosts, the present species was investigated in such a large number of fish that I could at least attempt to establish the statistical frequency of infection; for the sake of completeness, I then extended these calculations also to those host species represented only by a small number of individuals.

If we consider all investigated specimens of Gadus virens (with the exception of those which I infected experimentally), we find that approximately 56.7% of these fish were infected with M. bergense; this is without taking into consideration the provenance and age of the fish. If we take account of these two factors, we obtain the following interesting results: 40.9% of medium-sized individuals south of Trondheim were infected; north of this city, the value rose to 96.4%. Obviously, this change did not occur suddenly,

but only gradually; still, the much greater number of diseased individuals was noticeable already when I was collecting the fish just after Trondheim. The number of infected specimens then increased steadily northward, reaching a maximum at about Lofoten and then remaining fairly constant farther north. Very similar conditions were exhibited also by very young and very old fish (although for these groups I was able to examine only far fewer individuals): South of Trondheim ca. 8.8% of fish measuring 15-20 cm in length were infected; north of this city, nearly 100%. South of the limit, I did not find any fully grown (ca. 80 cm) infected fish (the few which were examined came from Bergen); to the north, 85.7% of an approximately equal number of large fish were infected. Although these latter figures are inexact because they are based on inadequate material, overall it is still clear that the rate of infection indisputably rises quite significantly towards the north, and this in all age classes. I have already touched upon this fact in a study published recently (7), in which I suggested the hypothesis that the higher rate of infection is connected with the fact that the fish are living closer together; for, this would greatly facilitate transmission of the parasite at least by means of its permanent spores. I still believe that this is a major reason for the above values, since as far as I know, G. virens is a northern fish, with its abundance increasing towards the north.

A very similar pattern is shown also by Gadus aeglefinus, which also often carries Myxidium bergense in its gall bladder. (However, the number of individuals examined was not as large as in the case of G. virens, and especially south of Trondheim only few fish were examined.) I found an overall infection rate of ca. 71.4% for this host. (The age of the fish was not considered.) In the South, i.e., approxi- 15
mately south of Trondheim, 15.7% were infected, but in the North, ca. 92.1%. In the North, the values for both hosts nearly corresponded, whereas in the South, G. aeglefinus seems to be infected more seldom. However, I was able to examine only 19 specimens in the South, so that in any case, with more material, this value could still change considerably.

It would probably be particularly interesting to study the conditions at different times of year and see whether they show a major influence upon the level of infection. In southern Norway, I undertook my studies in May, June, July, August and September, and I did not find any differences; however, there remains the winter, which may well have an influence. We know that such seasonal variations occur, e.g., in the case of Myxidium lieberkuehni BUETSCHLI and Henneguya psorospermica THÉL. in pike.

Among other hosts of Myxidium bergense, also Gadus callarias and Pleuronectes platessa were examined in large numbers. Both species seem to be only occasional hosts of this parasite. Approximately 2.7% of G. callarias were infected,

and ca. 7.1% of P. platessa. I shall also give the values for the remaining hosts now known, although these figures are less valid because the material investigated was inadequate: Sebastes viviparus 12.5%, Anarrhichas lupus 12.5%, and Gadus merlangus 14.3%.

I need not discuss further the occurence of Myxidium incurvatum THÉL., M. inflatum AUERB. and M. procerum AUERB., since I can not add anything new to my earlier remarks (1-6); hitherto on the Norwegian coast, all three of these parasites are known only from Bergen.

Molva vulgaris and Brosmius brosme were described earlier as hosts of Sphaeromyxa hellandi AUERBACH; to these I can now add Centronotus gunellus. This find extends the range of the parasite considerably, since the infected fish was caught near Torghatten; and in any case, as I have already reiterated, the parasite will be found wherever its hosts occur.

A parasite found very frequently in some Norwegian fishes is Zschokkella hildae AUERB., which I found in the urinary bladder of Gadus callarias, G. virens, G. aeglefinus and Phycis blennioides; its occurence in G. aeglefinus is new. Also this parasite appears to be distributed all along the coast of Norway, at least from Bergen on. The infection rates of its major hosts were approximately as follows: Gadus callarias ca. 68.4%, G. aeglefinus ca. 87.5%, and G. virens ca. 26.6%. These values seem to indicate a very marked preference for G. aeglefinus.

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I do not have many new observations to report concerning Leptotheca macrospora, parva, informis and longipes; essentially, I can refer to my earlier works (1-5). It should perhaps be noted also that I found L. macrospora AUERB. 1911 in Sebastes viviparus from Kristiansund, which extends its range considerably; that L. parva THÉL. was discovered in Scomber scombrus in Kristiansund and Stavanger as well as in Bergen; and that also Gadus merlangus (Tjömö 1911) may be considered a new host of L. informis.

With respect to certain, as yet undetermined, additional species of Leptotheca and Ceratomyxa which were found either only in juvenile vegetative forms or with the spores still undeveloped, I refer to Part II of this study, in which some discussion is devoted to these parasites.

It is very striking that Lentospora cerebralis (HOFER) PLEHN was found not even once in my investigations, although we always opened the skulls of all fish. If this parasite should continue to be unobserved, its absence in Norwegian waters would be an extremely interesting and remarkable fact.

Also Myxobolus aeglefini AUERB. did not occur by any means as frequently as in Gadidae in the North Sea. During my journey of 1911, I found this parasite only in four fish--three specimens of G. callarias from Abelvaer, Lödingen and Vardö, and one of G. aeglefinus from Abelvaer. This would correspond to an infection rate of approximately 2.2% for these two species. New hosts of the parasite were not found;

however, with the sites just named, its range was extended from the North Sea to the Arctic (Vardö), i.e., over the entire Norwegian coast. It is noteworthy also that G. virens seems to be immune to this parasite. Not a single individual which I examined was infected.

I had hoped that interesting conclusions could be reached also by considering the way of life of the fishes investigated; e.g., by dividing them into littoral, bathyal, and pelagic fishes. So far, however, such groupings have been unsuccessful, since the material for the pelagic and bathyal forms was inadequate. The solution of such questions must await future study.

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Finally, if we inquire which major groups of the Myxosporidia are most involved in making up the parasitic fauna of Norwegian marine fishes, we find what should have been expected from my earlier work (6): The Miktosporea are most numerous, with four genera in at least eight species. The Disporea, known exclusively as parasites of saltwater organisms, are almost equally represented (two genera in at least six species). As expected, the Polysporea are represented only by a single species, and the still somewhat uncertain Monosporea, known only in the Mediterranean, are completely absent.

To summarize briefly the facts reported in Part I, the most important theme is that the distribution of the parasites follows closely that of their hosts, but when

different fishes can serve as hosts, it may be very extensive, and in any case many species of Myxosporidia can be encountered everywhere at least along the European coast. For a number of forms this has already been demonstrated, and it is very probable that this number will be augmented further as time advances. Nor can we rule out the hypothesis that the range of distribution may even be much wider than we now assume; investigations on the coasts of other continents would probably bring such facts to light.

Now as regards specifically the distribution of the parasites along the Norwegian coast, it is, corresponding to the occurence of the host fishes, very uniform along the entire coast. Of course, I do not deny the possibility that fishes which are characteristic only of certain coastal sections may also carry in their organs parasites which occur only in these fish and may therefore also be restricted to these particular locations. Further investigations could easily bring this question closer to a solution.

II. Morphological--biological section 18

The data given in this section are the results of my investigations in 1911 compared with my earlier studies. The reader will find that some of my earlier data have been considerably expanded or supplemented by my new findings, whereas other data had to be revised or greatly modified. For, the more material is available, the clearer is our

understanding of the biology of our group of parasites, and much that we believed was clearly proven has to be adapted to the new slant.

The material used was generally preserved in 5% formalin, then transferred through gradations into absolute alcohol, embedded in paraffin, sectioned and stained with Giemsa. Sometimes I was surprised by the very good results of this type of treatment. Most of the specimens were so well preserved that even very fine details could be examined. The thickness of the sections was 5μ. They were examined with a Seibert's apochromatic oil immersion 2 mm objective and compensating ocular 18, with a magnification of approximately 2250 (artificial source of light); almost all the illustrations were drawn using an ABBÉ drawing apparatus with the same combination of lenses, and accordingly, unless otherwise stated, all are in the same proportions.

The material processed will be presented in the sequence described on p.4 in Part I.

1. Myxidium bergense AUERB.

I have already reported on the occurence of this parasite in new hosts in Part I. According to the data given there, we can probably consider this species as one of the most common and widely distributed parasites of all Norwegian fishes. The principal hosts appear to be Gadidae, and in particular, G. virens and G. aeglefinus, whereas the other fishes are only occasional carriers of this Myxidium.

The manner of its occurence in the gall bladder is apparently the same in all hosts; the parasite lives partly 19
as a free-swimming form in the bile, as I reported previously, but also sometimes is attached to the epithelium of the gall bladder by means of special pseudopodia; this gives rise to very characteristically shaped vegetative forms (Figure 22, Plate 2). Gadus virens is differentiated from the other hosts only by the severity of the infection. I have never yet seen any other fish in which the gall bladder was infected as severely as in Gadus virens. Therefore this can probably be designated as the major host.

With regard to the structure of the vegetative forms and of the spores, I have no new information, except that I was able to observe the mode of sporulation in its different stages. I will recapitulate the relevant findings on the following pages, and then attempt to reduce all of the other modes of spore formation published previously to a uniform pattern. We shall see that this can actually be done without very great difficulty. Of course, it must remain for the future to determine whether my thoughts on this theme are correct.

We know already from my previous investigations that Myxidium bergense is simultaneously monosporous, disporous, and polysporous, i.e., it represents a very typical mictosporous Myxosporidium. I was able to observe the same processes of sporulation again in 1911. First, we shall become acquainted with the mode of sporulation in the polysporous type; then the other types can be readily understood.

In contrast to Myxobolus, Henneguya, etc., and in correspondence with Ceratomyxa drepanopsettae AWER., a pansporoblast does not contain two spores; rather, each spore develops separately.

The process is initiated by the formation of first-order propagative cells (see KEYSSELITZ 14). A denser protoplasm staining dark blue with Giemsa settles around a large nucleus of the vegetative form, giving rise to cells ca. 4μ in diameter. These cells can divide, and thus create the second-order propagative cells. These are in no way different from the first-order cells. They usually lie together in groups of three (cf. Figures 1-4, Plate 2).

Now I believe, in agreement with AWERINZEW (8) and MERCIER (18), that these second-order propagative cells should be viewed as gametoblasts, and that they give rise to macrogametes and microgametes, which both are roundish, uninucleate cells, and differ only in their size (cf. Figures 5 and 6, Plate 2).

Macrogamete and microgamete come together and their plasma fuses (Plate 2, Figure 8). This plasmogamy need not proceed very quickly; the microgamete may still be separate from the macrogamete for a long time, even at a time when the nucleus of the latter is already dividing again (Figure 9, Plate 2) or conversely (Figure 9a, Plate 2). Usually the two gametes fuse simply by combining their plasma; however, it can also happen that the microgamete forms a cap over the

macrogamete (Figure 8a, Plate 2)[1]. This gives rise to figures corresponding exactly with KEYSSELITZ's (14) fig. 43, MERCIER's (18) fig. 15, and LO GIUDICE's (17) fig. 32. However, this type of apposition is not very frequent; usually we see only a small globe next to a larger one (Figure 8, Plate 2). Following the completion of plasmogamy, we then have a binucleate cell containing a large and a small nucleus. Unlike AWERINZEW and MERCIER, I did not directly observe a fusion of both nuclei, nor could I detect any figures indicating such a fusion. Rather, I believe that in our species, usually both nuclei remain separate and divide again immediately after the completion of plasmogamy, or even during the process (Figures 9-12, Plate 2). However, I consider it entirely probable that the other pattern, as well, occurs in our species (see below). During subsequent steps, there is also an emission of chromatin as described by AWERINZEW (8) (Figure 22, Plate 2), but in addition to this, a reduction seems to take place so as to form two structures resembling residual nuclei. For, we often see two intensely stained, roundish particles of chromatin in the sporoblast, usually near the surface, which I can only interpret as residual nuclei (Figures 11, 14, 16 and 18, Plate 2); we then find such structures also lying freely in the plasma of the vegetative forms.

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1. This figure also allows of another interpretation; the cell forming a cap may also be a shell cell which has already become differentiated very early. This view is indicated by the presence of a large, dark clump of chromatin, which probably represents a residual nucleus.

Nuclear division continues in the sporoblast until there are six nuclei (excluding the residual nuclei) which are no longer distinctly different in size. At first the sporoblast seems not to have a covering. The individual "cells" which make it up seem to maintain some degree of independence, just as in Cerat. drepanopsettae; for they arch out in the contours of the sporoblast and give it an irregular shape. The formation of the shell cells does not necessarily occur only after the completion of divisions in the sporoblast; such cells can already appear when only two or three nuclei, apart from them, are present in the sporoblast. Hence, the different parts of the sporoblast have a certain amount of scope in their development (cf. MERCIER 18). However, once the nuclear divisions are completed, we always find the typical figure of a new spore: on the outside, the shell cells with their nuclei, and on the inside, the binucleate amoeboid germ and two uninucleate polar-capsule cells (Figures 14-22, Plate 2). 21

If the reader will compare the illustrations given here with those of previous authors, he will find many points of agreement. My findings correspond best with those of AWERINZEW (8) and MERCIER (18); the only difference is that in those authors, the nuclei of the macrogamete and the microgamete fuse during copulation. The accuracy of my interpretation is witnessed by the fact that again in this investigation, I observed quite clearly in many cases that

the nuclei of the amoeboid germ fused in the completed spore. If LO GIUDICE (17) opines in his recent study that this karyogamy is an anomaly occuring only in parasites of dead fish, I must disagree categorically. SCHROEDER (20) observed this phenomenon not only in fish which had already long been dead, but also in freshly preserved specimens of Sphaeromyxa sabrazesi, in which he saw the two nuclei of the amoeboid germ come together and fuse. I found the very same pattern in Sphaeromyxa hellandi, Myxidium bergense, and Myxidium procerum, and it was always the older spores that were uninucleate (as can, of course, easily be judged from the development of the shell). Also, R. ERDMANN emphasized the fusion of the nuclei of the amoeboid germ in Chloromyxum leydigi (12), although her data can be doubted insofar as unstained objects were examined. Finally, I refer to my experiments infecting fish with Myxidium bergense. All those 22
specimens were fixed and studied freshly killed, and I can state confidently that normally, in many cases, a uninucleate cell finally arises through fusion of the nuclei of the amoeboid germ.

However, I do not believe that the difference between our respective views is very profound and essential. We both accept a fusion of the nuclei from both copulating cells, albeit at somewhat different points in time. AWERINZEW and MERCIER have the karyogamy follow directly upon the fusion of macrogamont and microgamont, whereas in my view and that of

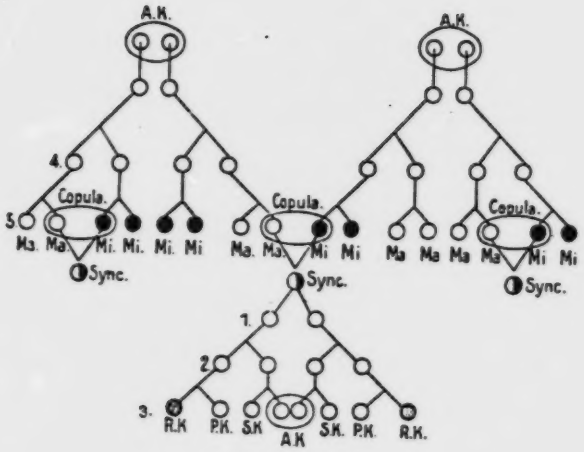

Figure A. Schema of monosporous sporulation without a plasmic residue. 1. Type no. 1. Synkaryon at the beginning of sporulation.
Key: Ma-macrogamete Mi-microgamete A.K.-amoeboid germ Sync-synkaryon R.K.-residual nucleus P.K.-polar-capsule nucleus S.K.-shell nucleus

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SCHROEDER (20) it takes place only later, in the completed spore, or even only in the free amoeboid. In either case, the nuclear elements present in the product of copulation are identical. It therefore seems to me very probable that both modes occur, and this even in the same species (see below). If such is the case, we are relieved at a stroke of many discrepancies which could not be explained previously. I believe that what happens is somewhat as follows: If a karyogamy does not occur at the start, then sporulation proceeds as I have just described; the synkaryon is formed only in the completed spore, or even later in the free 23
amoeboid germ, which then continues to develop in the familiar manner (Figure B).

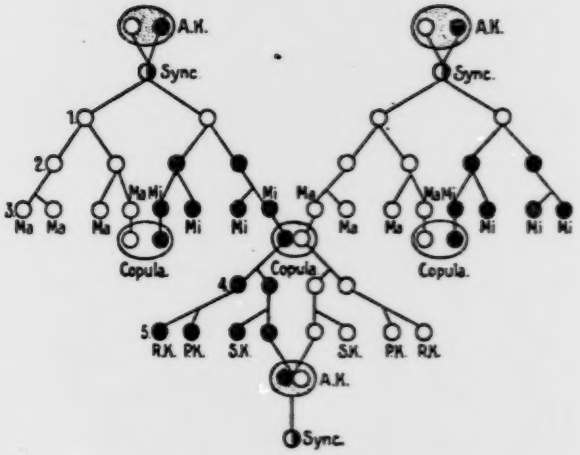

Figure B. Schema of monosporous sporulation without a plasmic residue. 2. Type no. 2. Synkaryon at the end of sporulation. Key: See Figure A.

However, if a synkaryon is formed directly at the beginning, then sporulation proceeds exactly as above, but with the differences described by AWERINZEW and MERCIER. In this case, however, there is no longer a fusion of the nuclei of the amoeboid germ, since of course they are already products of the division of the synkaryon. Instead, the amoeboids divide, at least after leaving the spore, and perhaps still within the spore, giving rise to uninucleate cells, which then still behave like other amoeboids (cf. Figure A).

If we assume that both patterns occur, we can explain the fact that the nuclei of the amoeboid germ do not fuse in all spores. I have encountered such cases repeatedly in my experiments with Myxidium bergense. Indeed I have occasionally

even found spores with four uninucleate amoeboid cells. 24
MERCIER (18) mentions identical observations, as does also AWERINZEW (8). Previously I considered these structures anomalous, but now I believe that they are part of the normal developmental process, and specifically of the type of sporulation with the karyogamy at the beginning, whereas spores in which the amoeboid germ becomes uninucleate are formed in the other manner. We shall have several opportunities to return to this question when comparing the processes which I describe with those of other authors; at present, I should like first to conclude my description of the processes in Myxidium bergense.

To summarise our results concisely, sporulation takes place in this species as follows: (1) Formation of first-order propagative cells. Their division to form second-order propagative cells (macrogametocytes and microgametocytes). Formation of the macro- and microgametes; plasmogamy of a macro- and microgamete. Further division of the nuclei of the sporoblast until there are six, with emission of chromatin and possible formation of two "residual nuclei". Differentiation of the components of the sporoblast into shell cells, polar-capsule cells and amoeboid germ. Maturation of the spore. Fusion of the nuclei of the amoeboid germ--synkaryon (possibly only in the stomach or intestine of a new host).--Or (2) formation of the first-order propagative cells, and their division leading to the formation

of the second-order cells (macrogametocytes and microgametocytes). Formation of macro- and microgametes and copulation of paired cells. Fusion of both nuclei to form a synkaryon. Division of the synkaryon and its daughter nuclei until there are six. Emission of chromatin or formation of residual nuclei. Differentiation of the sporoblast into its components (shell cells, polar-capsule cells, and amoeboid germ). The mature spore, with its amoeboid germ containing two nuclei, enters a new host as the amoeboid divides into two to four uninucleate cells. (In both sequences, I have assumed that, as in the case of M. bergense, the spores develop separately, i.e., completely independently. In forms with two spores in a pansporoblast, sporulation takes place as described by MERCIER 18 and SCHROEDER 20.) Cf. Figures A-E.

In polysporous and disporous Myxosporidia, sporulation seems to occur in this way. But what happens when a small vegetative form transforms completely into a spore, i.e., in monosporous development? I believe that such cases follow exactly the same pattern; at least there are indications that they do. In earlier works, I have described processes of plasmogamy between new germ cells emerging from the epithelial cells of the gall bladder. At that time, I believed that this was a plasmogamy of entirely vegetative forms. Now I must modify this assumption. I believe that these processes are closely related to monosporous reproduction, and that they are none other than the same processes which we observed taking place inside the parent organism in polysporous types, now happening freely in the bile.

25

The connection is probably as follows: When the young germ cells have fallen out of the epithelial cells of the gall bladder, they divide and form second-order propagative cells (figures 39 a-e in my monograph), which may form characteristic aggregates, and which next give rise to macro- and microgametes (figures 38 f and g in my monograph). These join in pairs and eventually fuse (figures 39 f and g of my monograph). Drawing 'h' of the same figure would then represent an already somewhat later stage, whereas 'i' would be a case in which the nucleus of the microgamete divides again already before the completion of plasmogamy (see above). We see how readily the processes described can fit into the sequence of my study of 1911. For the most part, my earlier observations were correct, but they were wrongly interpreted. I believe that with my present explanation I have come considerably closer to the truth.

My most recent investigations have now completed the life cycle of Myxidium bergense so that I can give a fully elaborated version of the reproductive cycle of this parasite. This cycle is probably as follows (Plate 3):

Spores are released, e.g., in the gall bladder of an infected Gadus virens, and pass with the bile through the bile duct and into the gut, and then with the feces into the open water. Here they drift freely and are taken up by a new host, either directly or clinging to another food particle. (On this question, see my study in Zool. Anz. vol. 39, 1912,

p. 617-623.) In the stomach of the host, they round off 26
their shape (under the influence of the gastric juice), and in many cases, the fusion of their two nuclei now occurs. Then, as the spores enter the intestine, their valves open. The polar filaments are ejected and the amoeboid germs are liberated. Probably their karyogamy is always complete at this stage, and the uninucleate germ cells creep actively up the bile duct. In the gall bladder, they penetrate the epithelial cells of the bladder wall for some time, perhaps for better feeding (ERDMANN). Eventually they pass back into the bile, and then begin their further development depending on the type of sporulation. Monosporous individuals first divide and form macro- and microgametes, which join in plasmogamy, and their copulation produces a single spore, without any residue. Disporous and polysporous individuals also originate from the uninucleate germ cells, either through simple growth with simultaneous division of the nucleus, or after the fusion of germ cells by plasmogamy; plasmogamy still occurs even with older individuals. Sporulation then takes place inside the parent in exactly the same way as with the monosporous types. Finally the spores are released and the cycle begins again. (This is the reproductive cycle for the type in which the synkaryon is formed in the mature spore; it applies to the other type mutatis mutandis.)

The only task remaining for us is to investigate whether the opinions published previously concerning sporulation in our group of parasites can be reconciled. If we

compare the structure of the vegetative forms, and especially that of the spores, in the different genera, we find that on the whole, a very uniform structure is predominant. Should it be different in the case of sporulation? I believe not, in spite of the apparently extremely different data of the different authors. If we compare their descriptions of sporulation, we encounter very important differences, but this is definitely not the case if we simply juxtapose their illustrations in a completely objective manner, arranging them according to similar appearance, without following the exposition. I have made such a comparison on Plate 4 considering the most relevant authors, and an experienced reader 27
will concede that a truly amazing essential correspondence prevails in this select arrangement, allowing, of course, for minor deviations due to the different genera and species. But if such is the case, i.e., if these objective illustrations, which correspond to the reality, can be correlated in such neatly matching series, should there not also be a plausible common explanation? I believe that there should, and I will therefore attempt in the following pages, on the basis of my earlier exposition, Plate 4, and the works of the authors cited on the plate, to construct what I believe to be a satisfactory general explanation of sporulation in the Myxosporidia. I should like to add that in addition to the sporulation of Myxidium bergense, I know personally and have studied in detail also that of Myxidium inflatum, Zschokkella

hildae, Sphaeromyxa hellandi, Sphaerospora divergens and Henneguya psorospermica. Finally, I should not neglect to mention that SHIWAGO (22) has already made a similar attempt, albeit only purely theoretically, and that he arrived at some of the same conclusions. The respective authors will be discussed in the same order as shown on Plate 4. Of course, I must presuppose that the reader is essentially acquainted with the different studies; I can describe their contents here only as far as suits our purpose.

1. AWERINZEW (8). As is well known, AWERINZEW based his investigations chiefly on a disporous Myxosporidium, Ceratomyxa drepanopsettae AWER. In addition, he also undertook control studies on mictosporous Myxidia. Accoding to A., we can differentiate in the vegetative forms two vegetative and two reproductive nuclei, which are still all derived from one original nucleus. The reproductive nuclei, by a rearrangement of the plasma, form two actual cells, the gametocytes, which divide into two macrogametes and two microgametes. These copulate in pairs, and after the plasmogamy, also karyogamy occurs, so that we then have in each amoeboid, in addition to the two vegetative nuclei, also two cells each possessing a synkaryon. Division of the synkaryon, and later also of the cytoplasm, gradually produces a number of very independent cells, which serve as primordia for the spore components (polar-capsule cells, amoeboid germ, and shell cells). The two shell cells of each spore originate

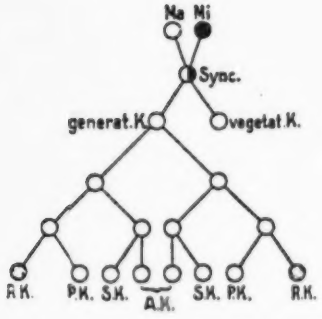

Figure C. Schema of monosporous sporulation with a plasmic residue and vegetative nucleus.
Key: See Figure A.

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from one cell which divides only later. During sporulation, 28
chromatin is released into the plasma of the vegetative form. Each spore develops completely independently; the sporulation need not be synchronous. Of the processes described, those shown on our plate are the first-order propagative cells (row 1) and their division (row 2), the gametocytes in division (row 3), copulation (row 4) and another division after copulation (row 5). This mode of sporulation corresponds entirely with the type which I described above with the synkaryon formed directly at the start of sporulation. Since there are no important differences between our views, we can be content with this brief description.

In another short study (9), the same author discusses similar processes in a Myxidium species. Also in this case our views nearly correspond. A's data differ from my findings only with respect to the development of the shell cells:

He gives the individual cells of the rudimentary spore greater independence. However, this discrepancy may be due to the fact that we investigated different species. Mictosporous Myxosporidia in general are known to vary considerably in their different vital manifestations. In any case, there is nothing in this study which could not be explained by my preceding discussion, so that we can confirm a very close accordance between A.'s views and mine. The processes of nuclear division in the monosporous type of sporulation observed also by A.--in which a plasmic residue of the vegetative form subsists--are explained by the schema in my Figure C. The sporulation of polysporous forms can be easily derived from this schema.

2. KEYSSELITZ (14). In constrast to AWERINZEW, KEYSSELITZ performed his investigations on a polysporous form, Myxobolus pfeifferi. It has long been known that in 29
these Myxosporidia, the spores are formed in pairs within a common pansporoblast, so that they are not as independent as in Ceratomyxa drepanopsettae. K. designates the earliest primordia of the pansporoblast as first-order propagative cells. These are uninucleate cells which divide mitotically and usually yield three second-order propagative cells. Their size varies from 4 to 9 μ in diameter. Each second-order cell becomes independent and divides again by abstricting a small cell. The latter forms a cap upon the larger parent cell. This pair of cells is known as a gametoplast. Next,

two such gametoplasts come together, and while the two large cells remain independent, the small, outer cells fuse and form an envelope around the inner cells, with their two nuclei usually adjacent to the contact surface of the two large cells. K. names this completed structure a sporocyst. The nuclei of the enveloping cells would correspond to the residual nuclei of previous authors. Now the two large cells of the sporocyst continue to divide until there are twelve uninucleate cells. Two pairs fuse, so that the contents of the sporocyst consist of eight uninucleate and two binucleate cells. The latter represent the amoeboid germs of the new spore, whereas the eight remaining cells become the two shell cells and the two polar-capsule cells. Also, chromatin is emitted within the sporocyst during cell division. This is a very crude outline of KEYSSELITZ's view; for details, I refer to the original study.

How well does this description accord with my own view? I must concede that they are irreconcilable. However, the situation is quite different if we consider only the illustrations of K., and if we also take account of the comments made regarding K.'s publication by MERCIER (18), who experimented with the same species. If we do this, we shall find outstanding harmony.

K. reports that the first-order propagative cells range from 4 to 9μ in diameter. Does this not imply that they are macro- and microgametocytes or macro- and microgametes?

MERCIER actually provides sufficient evidence of this. What K. interprets as division and the formation of gametoplasts (see figures 41-43 on his plate 13) is in reality the copulation of a macrogamete and a microgamete; I interpret K.'s figure 40 as the formation of microgametes from a microgametocyte. To any impartial observer, figures 41-43 will resemble an apposition of cells rather than their division. What K. explains as sporocysts, MERCIER interprets as sections through pansporoblasts in which the shell cells are already differentiated, and I believe that this is quite correct, since I myself have always seen such figures only in sections. Finally, the question should be asked how K. would apply his hypothesis of sporulation to those Myxosporidia which form only one independent spore, such as our Myxidium bergense. Indeed, since in discussing MERCIER's work we shall see that this author explains nearly the same figures in a way which can be harmonized most satisfactorily with my data and AWERINZEW's, I believe that MERCIER's opinion is more plausible; some points which remain obscure will be clarified when we discuss his work. 30

K. himself can not explain with his theory all of his figures. For example, he still finds figure 44 enigmatic. If the reader will examine row 5 on my Plate 4, he will see that all of the figures there are very similar. I have already stressed that the nuclei of macro- and microgametes can continue to divide before both structures are completely

fused--that is, if we have the type of sporulation in which the synkaryon is formed only in the mature spore. K.'s figure 44 is such a case, and corresponds to my Figure 9 on Plate 2 of the present study. I have no doubt that K. observed this type of sporulation, whereas MERCIER encountered both types simultaneously; I shall return to this fact when discussing the work of that author. With regard to the interpretation of K.'s figures, I refer again to MERCIER's work. I consider that the arguments asserted there against KEYSSELITZ are completely valid.

The result of our examination of the author just discussed is that his theory does not accord with ours, but his illustrations do not yield a single argument against our alternative interpretation; on the contrary, we can explain even those figures which K. could not explain. 31

3. MERCIER (18) performed his investigations on the same parasite as KEYSSELITZ. We have already seen on the preceding pages that he arrived at very different conclusions than that author, although his illustrations are extraordinarily similar to those of K. M. simply interpreted his findings differently, and I have already stressed repeatedly that my view accords completely with his. According to M., macro- and microgametocytes develop in the vegetative form and divide to form macro- and microgametes. A macrogamete and a microgamete fuse, with appearances which K. interpreted as gametoplasts. During the copulation, the nuclei fuse and form a synkaryon. This then continues to divide, and

eventually there are 14 nuclei in the pansporoblast, two of which should be viewed as residual nuclei. The other twelve then separate into two groups (sporoblasts): Two nuclei pass into the amoeboid germ, two become polar-capsule nuclei, and two become shell-cell nuclei. Quite in keeping with my new findings, M. already states that the differentiation of the shell cells can take place very early, and that in general, there is a certain amount of scope in sporulation. The two nuclei of the amoeboid do not fuse; rather, they continue to divide until finally four uninucleate cells arise from each amoeboid, which will further develop in the new host. This difference between M.'s view and mine has already been noted above and explained. Thus, I believe that both modes of sporulation can occur simultaneously in the same individual (cf. also the schemata in Figures A and B). My belief is confirmed also by findings which M. himself observed and illustrated. Figures 35-45 on M.'s plate 1 represent a different mode, as the author himself stresses. According to MERCIER, the binucleate stage in figure 35 arises from division of the synkaryon; however, no evidence is given for this statement. I believe instead that this figure represents the situation in which the nuclei of the macrogamete and microgamete do not fuse, but divide again directly (cf., e.g., fig. 35 with fig. 16 in MERCIER). The appearance of the nuclei is exactly the same as before the formation of the synkaryon, and it is maintained throughout. The figures also are exactly like those seen with Myxidium

bergense. I therefore believe that this view is at least as justified as the opposite view. In this case, then, we have both modes in the same species, and this may also explain the difference between some figures of MERCIER and of KEYSSELITZ. I believe that KEYSSELITZ's illustrations authorize the assumption that he observed only the second type; for his figures resemble MERCIER's figures 35-45 much more than figures 23-27 of that author. Added to this is the fact that in the second type, the karyogamy occurs only in the amoeboid germ, and in fact this was observed also by K., as is shown by his discussion in the text and figures 82-89 on plate 14. But therewith all apparent observational discrepencies between these two authors are eliminated, with the exception of their different interpretations; and this also constitutes fairly probable evidence that my hypothesis is correct. I have already referred several times in my discussion of K. to the arguments asserted--I believe appropriately--by MERCIER against his view. 31

To summarize concisely the preceding discussion, we arrive at the conclusion that there is no essential difference between MERCIER's explanation of sporulation and that which I have given, and that with a different interpretation, also KEYSSELITZ's findings can fit excellently into this framework.

4. SCHROEDER's (20) original study contained data concerning sporulation in Sphaeromyxa sabrazesi which can

be harmonized very well with the opinions of AWERINZEW, MERCIER and AUERBACH. S. finds large and small nuclei in the vegetative forms: A fair amount of plasma surrounds the large nuclei, while the small nuclei have only an indistinct plasmic areola. Both types can divide and thus increase in number. S. reports that a small nucleus penetrates the plasma around a large nucleus, creating one mass of cytoplasm with two different-sized nuclei. The nuclei do not fuse; rather, they continue to divide until there are 14. At this stage, there is a separation of the pansporoblast into two sporoblasts with six nuclei, leaving two residual nuclei. These sporoblasts give rise to spores in the familiar manner. Only then do the two nuclei fuse to form a synkaryon in the amoeboid germ of the mature spore.

We see already from this description that SCHROEDER's 33
original data almost exactly correspond with my present observations on Myxidium bergense, and specifically with the type of sporulation in which a synkaryon is formed at the end of sporulation. S.'s report accords nicely also with the views of the other two authors mentioned above, if we consider the other type. The large nuclei with their plasma after the division are the macrogametes, and the small nuclei are the microgametes. The binucleate phase is copulation. The differences in SCHROEDER's illustrations are only superficial; they are due to the wide-meshed alveolar structure of the plasma in his species.

However, in a later study (21), SCHROEDER revised his theory after KEYSSELITZ, and decided that the binucleate stage arose by division from the uninucleate stage, and therefore corresponded with K.'s gametoplasts. Two of these gametoplasts would then come together and form a sporocyst. I believe that SHIWAGO (22) was completely justified in rejecting SCHROEDER's change of view. Quite apart from the fact that figure 5 in S.'s second study can also be explained simply as an accidental copulative apposition, an entire series of figures (as S. himself admits) became inexplicable on his revised view (figures 8-16 of the first study), whereas they fit easily into the pattern of the other theory. The same applies to figures 9 and 10 in the second paper, which are readily explained by my presentation above, and would be identical with Figure 9 on my Plate 2. Figures 1-3 in S.'s new study would then represent divisions of first-order propagative cells, as I indeed also assume, while figures 6 and 7 could be explained by the way in which the sections were cut, or, in the case of total preparations, by their position in the specimen (cf. MERCIER's comments regarding similar figures of KEYSSELITZ). If these figures were prepared from sections, in any case the sections came from immature spores. I also saw such pictures, and was able to determine this explanation. (See also under Sph. hellandi.)

Thus, in SCHROEDER's works, we have a choice of two opinions. One view corresponds completely with the views of

AWERINZEW, MERCIER, and myself, and can readily explain all the phenomena. It was also formulated independently and in the first instance by SCHROEDER. The second seems to have developed subsequently under the influence of studies by KEYSSELITZ (14) and HARTMANN (13); it is supported by a 34
minority of the figures, and can not explain a good number of facts. Therefore I do not consider it unjustified to decide in favor of the earlier view, especially since also the figures which I found in Sphaeromyxa hellandi seem to favor this view much more strongly. But once this decision is accepted, then also SCHROEDER's explanation falls very neatly into the cycle which I have described for the sporulation of Myxosporidia.

5. LO GIUDICE (16,17) is the last author whose work I shall briefly discuss. With my inadequate knowledge of Italian, naturally I can not take the liberty of describing his study in detail. I can only state that my impression leads me to conjecture that this author is more in agreement with KEYSSELITZ, although he seems to assume that a sporocyst can arise by division even from a single gametoplast. If we consider only the figures, they are all stages which were illustrated sometimes by KEYSSELITZ and also by MERCIER, so that we can at any rate assume that sporulation proceeds in Myxobolus ellipsoides exactly as in M. pfeifferi. LO GIUDICE apparently opposes the reports by MERCIER and myself of karyogamy occuring in the amoeboid germ; according to my

present view, this only demonstrates that he observed the other type of sporulation in his parasite, as did MERCIER. For the rest, I can refer to all of my remarks above regarding KEYSSELITZ.

However, I should also like to take the liberty of commenting on other parts of LO GIUDICE's exposition. First, as regards this author's method of experimental infection, I can not judge it unobjectionable. He employed a method which THÉLOHAN (23) already rejected as unnatural and inappropriate (abstricting an intestinal loop and injecting it with spores); it is obvious that in this kind of experiment the spores neither follow their natural route nor enter their natural environment.

I have never considered the rounding of the amoeboid germ before its emergence as a manifestation of spore-maturation; instead, exactly like our author, I trace it to the influence of chemical agents--in my case, the stimulation of the gastric juice and intestinal secretion.

Now a few words regarding the new species Coccomyxoides tincae LO GIUDICE: First, as regards the few illustrations of 35
sporulation, these do not show anything which could not be explained on my interpretation; it appears to be a polysporous or mictosporous? Myxosporidium in which the spores develop independently, as in Ceratomyxa drepanopsettae, Myxidium bergense, etc.[1] Thereby, however, I view its combination

1. The author does not recognize my new system of the Myxosporidia, but only cites the old system proposed by DOFLEIN (10,11).

with the genus Coccomyxa LÉGER et HESSE to form a family, as completely unjustified. According to our current knowledge of Coccomyxa, it is monosporous, and specifically of the type in which there is no plasmic residue in sporulation; moreover, it lives freely in the bile of marine fishes. Coccomyxoides, on the other hand, is polysporous or mictosporous? and forms cysts in the gills of a freshwater fish. Is it justified to unite these two genera merely because both have spores with one polar capsule? I do not believe that we should do this yet, especially since we already know of other polysporous forms with only one polar capsule. Accordingly, I think it much more suitable to classify the new genus provisionally under the Polysporea, and perhaps preferably between Lentospora and Myxobolus. At least for the present, I do not find its annexation to Coccomyxa admissible. (Of course, all of the preceding exposition is subject to the reservation that as a result of incorrect translation, I may have misinterpreted the opinions of the author.)

To conclude our discussion with a brief summary of the viewpoints which have emerged, a uniform pattern of sporulation in Myxosporidia can be sketched somewhat as follows:

Sporulation can proceed according to two different basic patterns. In one type, each spore develops completely on its own, and indeed, sometimes only one spore is formed (monosporous type). In the other, each primordium

(pansporoblast) gives rise to a pair of spores, which are therefore closely related in their origin (disporous type). I believe that the monosporous type is the more primitive and the disporous type evolved from it gradually through further division of the nuclei of the pansporoblast (cf. Figures A-E).

The monosporous type, in turn, can be divided into two subtypes: Either two, or even many, spores develop in a vegetative form, or else each myxosporidium produces just a single spore. In the latter case, either the entire parent organism is mustered in sporulation (Coccomyxa, Myx. bergense, etc.), or else a plasmic residue subsists (Chloromyxum cristatum etc.). Whereas in the disporous type, each parent holds at least two, but usually very many spores, produced in pairs. 36

In all these different types, the actual formation of the spores seems to proceed according to a uniform ground plan; only, we find differences in the time when the synkaryon is formed. These differences determine two very similar modes of sporulation:

(1) The synkaryon is formed at the beginning of sporulation. We first find in the vegetative forms vegetative and generative nuclei. The latter produce first-order propagative cells, which increase in number by division and then become the second-order propagative cells. These are differentiated into macrogametocytes and microgametocytes, which then divide to form macro- and microgametes. A

macrogamete and a microgamete copulate, and during copulation the two nuclei fuse to form a synkaryon. This divides again into 8 (monosporous type) or 14 (disporous type) nuclei[1], two of which in either case should be designated as residual nuclei. In addition, also chromatin is ejected into the cytoplasm of the parent organism (or to the outside?). The 6 (or 12) remaining nuclei and their cytoplasm now convert in the familiar manner into one or two spores having binucleate amoeboid germs. When a spore enters a new host, the nuclei of the amoeboid divide again and it breaks up into four uninucleate cells, which are released and develop into new myxosporidia (cf. Figures A-E and the reproductive cycle on Plate 3).

(2) The synkaryon is formed at the end of sporulation. The initial phenomena are exactly as in the first mode. However, a fusion of the nuclei does not occur during copulation; rather, the nuclei continue to divide until they number 8 (monosporous type) or 14 (disporous type)[1]. The process then 37
continues just as in (1); once again, the amoeboid germ in the spore is binucleate, but when the spore matures or the amoeboid departs into a new host, the two nuclei fuse and finally form the synkaryon, so that now only one uninucleate amoeboid emerges from each spore. The amoeboids can then continue to divide and develop as already described in detail above (cf. Figures B and E and Plates 2 and 3).

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1. In species with four polar capsules, the number of nuclei is augmented correspondingly.

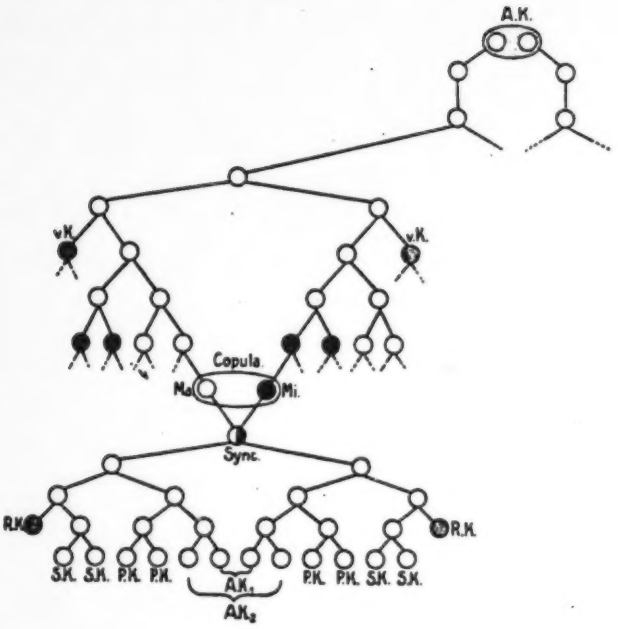

Figure D. Schema for a polysporous Myxosporidium in which two spores are formed in a pansporoblast. Type no. 1. Synkaryon at the beginning of sporulation. A.K.-amoeboid germ v.K-vegetative nuclei Ma-macrogametes Mi-microgametes R.K-residual nuclei A.K1-nuclei of the first new amoeboid germ A.K2-nuclei of the second new amoeboid germ S.K-shell nuclei P.K-polar-capsule nuclei Sync-synkaryon For the sake of simplicity. not all nuclear divisions are shown.

It is also a common feature of both modes that the different parts within a pansporoblast can be either loosely or closely related. In the former case, the spore primordia are individual cells from the start, and occasionally they can even be located far apart (AWERINZEW 8). In the latter, the nuclei are embedded in a common mass of cytoplasm, which divides into cells only later. 38

Now as regards the interpretation of all these processes, there can be no doubt that they represent sexual acts. If we complete the figures in my text in every detail, we shall find that in many cases, these phenomena should be interpreted as autogamy, but in others, also as heterogamy (as defined by SCHROEDER). The latter almost certainly applies to free-living forms in the bile, if amoeboids from spores of different parent organisms infect a new host simultaneously and the gametes of these different individuals copulate (see Figures A and B). However, as we can see from these same figures, the very same process can take place at the same time as autogamy. 39

Herewith I shall conclude my discussion of sporulation. I should like to emphasize again that I have given the version which seemed to me most understandable on the basis of my own experience and with consideration of the other most relevant studies. It must remain for further investigations, and for the future to determine my accuracy. In my case, my theory provides the first uniform explanation of sporulation applicable to all groups of Myxosporidia.

2.3.4. Myxidium inflatum, incurvatum, and procerum

With reference to the morphology and biology of these three species, I can not add to my earlier exposition. It should only be noted as regards M. inflatum that I followed the course of sporulation also in this species, and that it

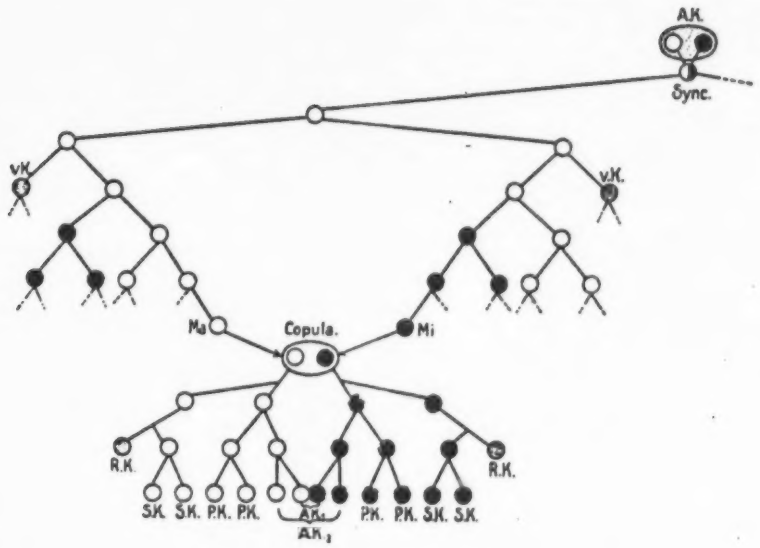

Figure E. Schema for a polysporous Myxosporidium in which two spores are formed in a pansporoblast. Type no. 2. Synkaryon at the end of sporulation. A.K-amoeboid germ v.K-vegetative nuclei Ma-macrogametes Mi-microgametes R.K-residual nuclei A.K1-nuclei of the first new amoeboid germ A.K2-nuclei of the second new amoeboid germ S.K-shell nuclei P.K-polar-capsule nuclei Sync-synkaryon For the same of simplicity, not all nuclear divisions are shown.

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seems to me to correspond with the pattern observed in Myxidium bergense (cf. Figures 23-28, Plate 2).

5. Myxidium oviforme PARISI

Unfortunately, I can not provide many new data concerning this new parasite, since, like PARISI (19), I have never seen vegetative forms with developed spores. The amoeboids which I saw were small, mostly globose, and 10-12μ in diameter. Occasionally figures were seen indicating the occurence of monosporous sporulation.

The spores which I found match PARISI's description exactly; they are 12-13μ long and 8-9μ wide, and their polar capsules measure ca. 4μ in diameter. The shell is endowed with ridges (cf. Figure 5, Plate 5).

Occurence: gall bladder (and perhaps also liver bile ducts) of Coris julis GTHR., Apogon rex-mullorum CUV., Gadus callarias L. and Trutta solar L.

Provenance: Vicinity of Naples (PARISI 19), Bergen, Kristiansund, Abelvaer, Rossfjord, Hammerfest and Vardö (AUERBACH).

6. Sphaeromyxa hellandi AUERB. 40

Previously I had always seen the vegetative form only in relatively large fragments. However, this time I found it entire in the gall bladder of Centronotus gunellus. It is shaped like a round, flat disk, and lies somewhat curled in the bladder (cf. Figure 1, Plate 5). I have already previously described its microscopic fine structure; I need not add to that description. The thickness of the disk is ca. 100μ.

With the present specimen I was able to follow all stages of sporulation. However, after my preceding discussion in connection with Myxidium bergense, I need not describe these stages here in detail. I should only like to note that the process corresponds fully with the description first given by O. SCHROEDER (20); i.e., the species is a

Myxosporidium with the disporous type of sporulation, following the second mode, in which the synkaryon develops only at the end of sporulation. I can confirm the latter feature, in particular, quite definitely. As I have already mentioned above, I also found figures corresponding to figures 6 and 7 in SCHROEDER's second study, which he considers sporocysts. I believe that I can state definitely that these figures are cross sections through rudimentary spores. The two large nuclei belong to the amoeboid germ, and the small, outer nuclei are those of the shell cells. I have also seen such structures in which a very small piece of the primordium of the polar capsule was included, thus probably confirming the validity of my assumption. One could also very easily imagine, for example, a section through figures 33 and 34 of plate 15 in SCHROEDER's first work, which would appear almost exactly like figure 6 or 7 of the second study.

Occurrence: gall bladder of Molva vulgaris, Brosmius brosme and Centronotus gunellus.

Provenance: Vicinity of Bergen, Torghatten.

7. Zschokkella hildae AUERB.

As already mentioned in Part I, large numbers of this parasite were found on my expedition last year. The vegetative forms sometimes drift freely in the urinary bladder, but sometimes also are attached to the walls of the bladder. 41
In the former case, they form relatively long, lobate

pseudopodia, whereas the pseudopodia of attached individuals are highly characteristic, and very reminiscent of the similar pseudopodia of Myxidium bergense. This can also lead to directly stalked individuals (Figure 2, Plate 5). Their size, and also the kind of sporulation are very variable. Sporulation is of the monosporous type with the synkaryon formed at the end. Monosporous sporulation with and without a plasmic residue has been observed, but also di- and even polysporous sporulation (with a maximum to date of four spores per individual). Thus, this species proves to be a very typical mictosporous Myxosporidium.

I can pass over sporulation itself, I have already described it earlier. Also in Zschokkella macro- and micro-gametes occur, either in the parent organism or freely in the bile (exactly as in Myxidium bergense). The illustrations in figure 1 of my earlier study (3) should be interpreted as stages of monosporous sporulation without a residue (see above under Myxidium bergense).

The spores show extraordinarily wide variation in size, ranging from 16 to 28.8μ long and 13-18μ wide. However, they always have the typical shape. On one occasion I encountered a spore with its sutural line extending straight across (Figure 3, Plate 5).

Occurrence: Urinary bladder of Gadus callarias, G. virens, G. aeglefinus and Phycis blennioides.

Provenance: Along the entire Norwegian coast.

8. Sphaerospora divergens THÉL.

I have encountered this apparently rare parasite only once, living freely in the urinary bladder of Hyppoglossoides limandoides. The vegetative forms, which drift in the urine, are roundish or oblong, with an average size of ca. 50 x 20μ. The outside shows a fine-grained ectoplasm. However, very many specimens are also found attached to the bladder wall, and they then extend ectoplasmic processes at the point of contact.

I was able at least to trace the broad outlines of sporulation, and I found it in accord with our views. The macrogametes and the microgametes are distinctly differentiated. The former measure ca. 5-6μ in diameter and possess a large, 42
light nucleus with a wide-meshed nuclear reticulum and a very prominent nucleolus; the latter are smaller, ca. 3μ in diameter, and have a more compact, intensely staining nucleus. During copulation the two nuclei can be distinguished very clearly by their appearance. I could not determine definitely which mode of sporulation occurs, but I believe that it is the second, with the synkaryon formed in the mature spore. Most individuals are polysporous; however, I believe that I have also found evidence of purely monosporous reproduction. It was not completely clear whether the polysporous individuals initiate the monosporous or disporous type, but I suppose--and many figures indicate--that both modes are possible; for, sometimes mature and immature spores

lie together in pairs, and the residual nuclei also can be seen; but sometimes they are also completely separate, and these spores forming in a purely monosporous way indicate that the monosporous mode is also possible.

Viewed on the surface, the spores are almost circular and measure ca. 10μ in diameter. Their thickness is ca. 8μ, and the polar capsules are ca. 4μ long. The two polar capsules diverge outwards, as the name implies. The shell is finely striate (Figure 4, Plate 5).

LABBÉ reproduces the spore of this parasite incorrectly in fig. 150 on p. 86 of his "Animal Kingdom" (15): He represents it as if there were an anterior triangular process of the shell between the two polar capsules, as, e.g., in Myxobolus pfeifferi etc. This is not the case; rather, plasma of the amoeboid germ is found at this site, as can be clearly seen in my Figure 4 on Plate 5 and THÉLOHAN's fig. 13, plate 7 (23).

Occurrence: Kidney tubules of Blennius pholis L., Crenilabrus melops L. and Cr. pavo C.V., urinary bladder of Hippoglossoides limandoides.

Provenance: Concarneau and Roscoff (THÉLOHAN 23), Naples (PARISI 19), Smalfjorden in Tanafjord (AUERBACH).

9.10.11.12. Leptotheca macrospora AUERB., parva THÉL., informis AUERB., and longipes AUERB. 43

I can not add to my earlier discussion of these four species. I shall therefore restrict myself to listing here again the occurrence and provenance of these parasites.

Leptotheca macrospora AUERB. Occurrence: Gall bladder of Sebastes viviparus and S. dactylopterus.

Provenance: Vicinity of Bergen, Kristiansund.

Leptotheca parva THÉL. Occurrence: gall bladder of Scomber scombrus.

Provenance: Marseilles, Le Croisic, Le Vivier (THÉLOHAN 23), Kristiansund, Stavanger, Bergen (AUERBACH).

Leptotheca informis AUERB. Occurrence: gall bladder of Molva vulgaris and Gadus merlangus.

Provenance: Bergen, Tjömö (AUERBACH).

Leptotheca longipes AUERB. Occurrence: gall bladder of Brosmius brosme.

Provenance: Bergen (AUERBACH).

In Bergen at that time I had found vegetative forms of a disporous Myxosporidium in the gall bladder of Gadus merlangus. I could not definitely determine the species, since it did not yet contain any mature spores. Upon reexamining this species, I now am fairly certain--based on an analogy with L. informis AUERB., which indeed, according to our data above, also was detected in these fish--that it represents the genus Leptotheca. Of course, I can not make this assertion with absolute certainty, since the spores were still somewhat too immature. The possibility should be borne in mind that it could also be a species of Ceratomyxa. For, also this genus parasitizes G. merlangus. Dr. O. SCHROEDER kindly sent me from Abbazzia some gall bladders of this fish

rather severely infected with a Ceratomyxa species. I believe that it is C. pallida THÉL.; at least, the data concerning the vegetative forms and the dimensions of the spores correspond with those of the species which I have. Since no illustrations of its spores have yet been published, I have reproduced them in Figure 9 on Plate 5. Their measurements are: length ca. 35μ, width ca. 6μ, polar capsules ca. 2-3μ(in diameter). The vegetative forms are roundish, disporous, ca. 14μ long and 10μ wide. As I have stated, it can not definitely be determined which of these two species the parasite from G. merlangus in Bergen represents, but I am more inclined towards L. informis. At any rate, it should be noted carefully in future whether C. pallida THÉL. will not be detected also in northern specimens of G. merlangus. According to our present knowledge, such an eventuality can be expected. 44

13. Ceratomyxa drepanopsettae AWERINZEW

It can never be determined easily or certainly that a parasite belongs to this species, since AWERINZEW (8) did not actually provide exact descriptions of the vegetative forms and spores. Therefore I can publish my findings in this connection only with strong reservations. I suppose that the parasites which I found represent the present species, because they were also found in the gall bladder of flatfish, and because the vegetative forms show a good correspondence with A.'s illustrations:

The outer shape of the amoeboids varies greatly. Some are roundish, some are irregular, and some even have a long stalk (cf. Plate 5, Figure 6). I could not observe a differentiation of ectoplasm and endoplasm. However, the two vegetative nuclei are distinctly different from the generative nuclei. I was not able to follow sporulation in detail, since the fixation in formalin was not completely unobjectionable. However, the figures which I saw seem to correspond well with AWERINZEW's drawings (8). For all of these reasons, I consider it permissible to conclude that the same species is involved in both cases.

In Part I, I expressed doubt as to whether the specimens of Ceratomyxa found in Pleuronectes flesus from Tjömö also belonged to this species. As far as I can see at present, the vegetative forms do not exhibit any deviations. The differences in the spores may be individual.

Spores of our parasite in a mature state were previously completely unknown. A. always observed only immature spores. I too encountered only very few completely mature spores, and I have therefore attempted to construct an approximate ideal pattern from my observations (Plate 5, Figure 7a). However, in the bile of Pl. flesus I found several mature spores. One of these is represented in Figure 8 on Plate 5. We can see that the differences in shape compared to Figure 7a are not important, so that both can probably be 45
derived from the same species. Dimensions: length of the spore

(along a cord from one tip to the other) ca. 56µ; width along the sutural line ca. 12-14µ; diameter of polar capsules ca. 4-6µ. Length of the cavity containing the amoeboid germ ca. 34µ.

Occurrence: gall bladder of Pleuronectes platessa, P. flesus, Drepanopsetta platessoides, Hippoglossus vulgaris and Hippoglossoides limandoides.

Provenance: Murman Coast (AWERINZEW 8); Kabelvaag, Rörvik, Tjömö (AUERBACH).

14. Ceratomyxa sphaerulosa THÉL.

I have no new observations regarding this species. The same applies to

15. Myxobolus aeglefini AUERB.,

which I found in Bergen, Abelvaer, Lödingen and Vardö.

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Translation of titles

1. Remarks concerning Myxosporidia
2. Report on a research expedition to Bergen, Norway
3. Sporulation in Zschokkella and the system of the Myxosporidia
4. Studies on Cnidosporidia
5. The Cnidosporidia
6. Our present knowledge of the geographic distribution of the Myxosporidia
7. Remarks concerning the mode of infection of marine fish by Myxosporidia
8. Studies on parasitic Protozoa. I. Sporulation in Ceratomyxa drepanopsettae mihi
9. idem. VII. On sporulation in Myxidium sp. from the gall bladder of Cottus scorpius
10. Protozoa as parasites and pathogens: presented from biological viewpoints
11. Manual of protozoology... 1909 and 1911
12. To the life history of Chloromyxum leydigi, a mictosporous Myxosporidium, Part I
13. Autogamy in protists and its importance for the question of fertilization
14. The development of Myxobolus pfeifferi 47
15. Sporozoa, in: Animal Kingdom, fasc. 5
16. On the development of Myxobolus ellipsoides THÉL.
17. Studies on Cnidosporidia
18. Contributions to the study of sexuality in the Myxosporidia
19. First contribution to the geographical distribution of Myxosporidia in Italy
20. Contributions to the developmental history of Myxosporidia. Sphaeromyxa labrazesi (LAVERAN et MESNIL)

21. On the primordium of the sporocyst (pansporoblast) in Sphaeromyxa sabrazesi (LAVERAN et MESNIL)

22. The current state of the question of the sexual processes of Myxo- and Microsporidia... Moscow 1911

23. Studies on the Myxosporidia

Explanation of the illustrations 48

The figures on Plates 1, 2, 3 and 5 are reduced by half compared to the originals. Plate 4 is reproduced in the original size.

Plate 1. Map of the Norwegian coast, showing stations where fish were caught.

Plate 2. All figures are sketched with a SEIBERT apochromatic oil immersion obj. 2 mm, comp. oc. 18 and an ABBÉ drawing apparatus.

Fig. 1-23. Sporulation of Myxidium bergense AUERB.

Fig. 1-4. First-order propagative cells and their division.

Fig. 5. Macrogamete. Fig. 6. Microgamete.

Fig. 7. Divisions of microgametes.

Fig. 8. Copulation of a macrogamete and a microgamete.

Fig. 9. Divisions of the nuclei during copulation; a-division of the nucleus of the microgamete.

Fig. 10-21. Further stages of sporulation; early primordia of shell cells at different ages in Fig. 13-15.

Fig. 20. Mature spore with synkaryon.

Fig. 22. Section through a vegetative form attached to the wall of the gall bladder.

Fig. 23-28. Stages of sporulation in Myxidium inflatum AUERB.

Fig. 23. Macrogamete.

Fig. 24. Microgametes.

Plate 3. Schematic reproductive cycle of Myxidium bergense AUERB. 49

Row 1. Purely monosporous development without plasmic residue, with the synkaryon formed in the mature spore.

Row 1a. The same, with the synkaryon formed at the beginning of sporulation.

Row 2. Polysporous development with the synkaryon formed in the mature spore. Sk-synkaryon.

Plate 4. Comparison of similar stages of sporulation as illustrated by the authors cited in the study. (The numbers shown for individual drawings are those of the figures of the different authors.)

Row 1. First-order propagative cells.

Row 2. Divisions of first-order propagative cells.

Row 3. Divisions of microgametocytes (or also microgametes?).

Row 4. Copulation of two gametes.

Row 5. Divisions of individual nuclei of gametes during plasmogamy or shortly thereafter.

Plate 5.

Fig. 1. Vegetative form of Sphaeromyxa hellandi AUERB. in the gall bladder of Centronotus gunellus (section). SEIBERT ap. obj. 16, c. oc. 8. ABBÉ drawing apparatus.

Fig. 2. Vegetative form of Zschokkella hildae AUERB. with a spore. Total preparation. SEIBERT ap. imm. 2 mm. c. oc. 18. ABBÉ drawing apparatus.

Fig. 3. Anomalous spore of Zschokkella hildae AUERB. SEIBERT ap. imm. 2 mm, c. oc. 18.

Fig. 4. Spores of Sphaerospora divergens THÉL. from the urinary bladder of Hippoglossoides limandoides. SEIBERT ap. imm. 2 mm, c. oc. 18. ABBÉ drawing apparatus.

Fig. 5. Spores of Myxidium oviforme PARISI from the gall bladder of Gadus callarias. SEIBERT ap. imm. 2 mm, c. oc. 18. ABBÉ drawing apparatus.

Fig. 6. Vegetative forms of Ceratomyxa drepanopsettae AWERINZEW? from the gall bladder of Pleuronectes platessa. Total preparation. SEIBERT ap. obj. 4 mm, c. oc. 8. ABBÉ drawing apparatus.

Fig. 7a. Reconstructed ideal spore of Ceratomyxa drepanopsettae AWERINZEW?

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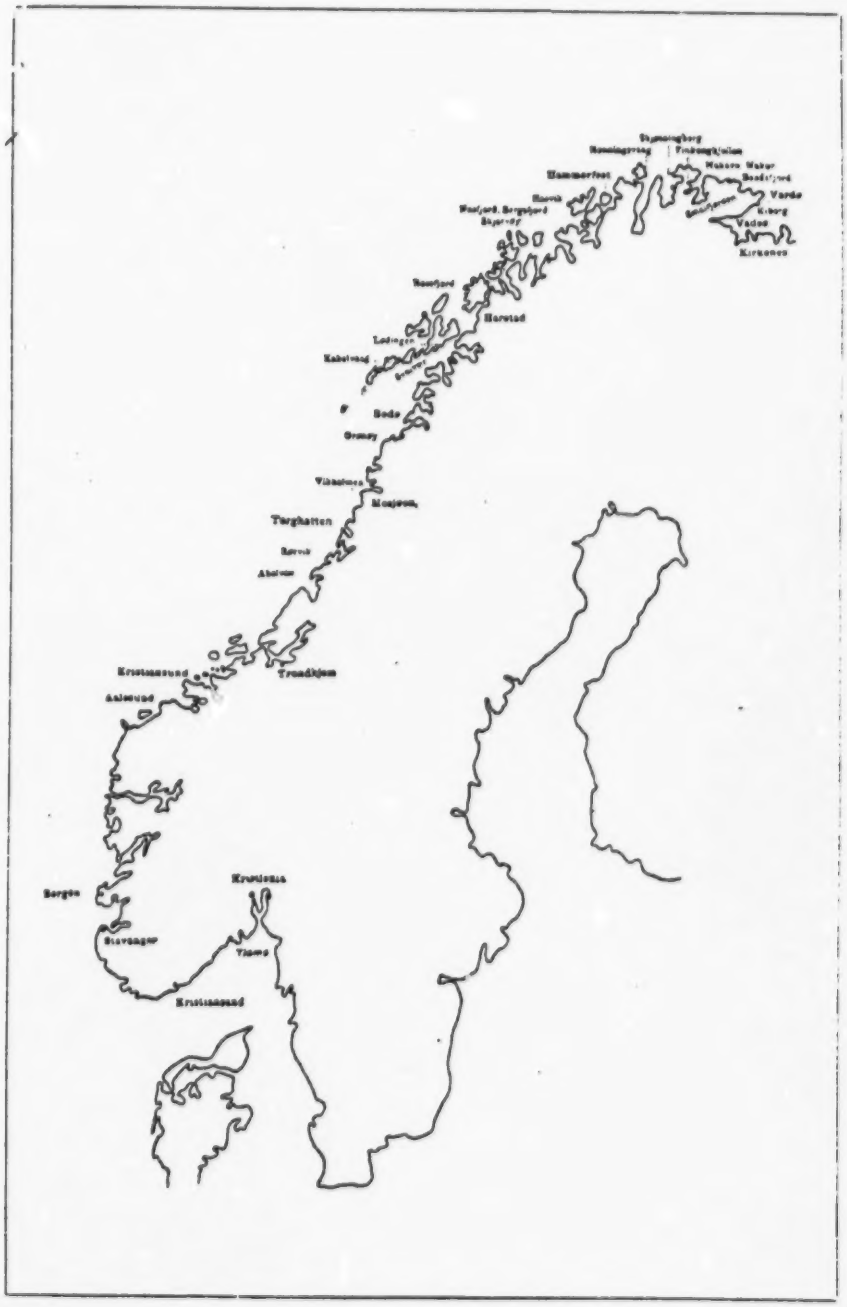
Fig. 7b. Young spore of C. drepanopsettae AWERINZEW. From the gall bladder of Hippoglossoides limandoides. SEIBERT ap. imm. 2 mm, c. oc. 8. ABBÉ drawing apparatus.

Fig. 8. Spore of C. drepanopsettae AWERINZEW? from the gall bladder of Pleuronectes flesus. SEIBERT ap. imm. 2 mm, c. oc. 8. ABBÉ drawing apparatus.

Fig. 9. Spores of Ceratomyxa pallida THÉL.? from the gall bladder of Gadus merlangus. Abazzia. SEIBERT ap. imm. 2 mm, c. oc. 18. ABBÉ drawing apparatus.

Plate 1.


Hammerfest
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Vikebukt
Mosjøen
Trøghatten
Trondhjem
Kristiansund
Ålesund
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Kristiania
Stavanger
Ytterø
Kristiansand